

STYLAGROSTIS A NEW SUBSECTION OF GENUS CALAMAGROSTIS
(POACEAE: POOIDEAE) AND THREE NEW SPECIES
FROM COLOMBIA, ECUADOR AND VENEZUELA*

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INTRODUCTION

The genus Calamagrostis Adans., (Poaceae: Pooideae), is heterogeneous with about 250 species, distributed worldwide (Bjoerkman, 1969; Chase and Niles, 1962; Clayton and Renvoize, 1986) including approximately 70 poorly known species in the páramo and puna of south America.

"Identification of Calamagrostis species is difficult, not only because of the large number, but because of the limited variety of of characters distinguishing the species" (Stebbins, 1930). As a consequence a multitude of species, varieties, and forms have been described, these differ only in minor morphological details, that may be a response to the environmental conditions. Interspecific hybridization is common in the genus Calamagrostis and "large numbers of supposed hybrids have been described" (Clarke, 1980). Many studies have shown that the taxonomic complexity within the genus is due to apomixis, introgressive hybridization, and polyploidy (Nygren, 1948, 1954a, Tateoka, Hiraoka and Tateoka, 1977). Therefore further studies are necessary in order to clarify the species relationship within the genus Calamagrostis and with closely related genera within the tribes Agrostideae and Aveneae. The genus Calamagrostis is similar to the genus Agrostis to the extent that Wasiljew (1960) considered no definite boundaries existed between them. Bjoerkman (1969) stated that it "is difficult to draw a sharp limit between Agrostis and Calamagrostis, if possible at all." The separation of Calamagrostis and Deyeuxia as genera, based on the prolongation of the rachilla and callus hair length in relation to the lemma, have been considered insatisfactory in a world context. There is still controversy as to generic boundaries for the South American species, but this will not be clarified until further studies of the genus Calamagrostis based on biochemistry, cytology, morphology, anatomy, and biogeography are done. It is hoped that this preliminary work will be a contribution in helping to understand the complicated taxonomy of this genus.

This investigation follows Koch, 1837 (cited by Wasiljew, 1960) who classified the genus Calamagrostis into two sections: Epigeios Koch, lacking the rachilla of a second floret, including the species from the old world; and Deyeuxia (Clar. ex Beauv.) Reinchenb., presenting the rachilla including the species from the

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new world, admitted by some authors as a genus Deyeuxia Beauv. until further revision of the genus Calamagrostis and their related genera is done.

The lemma (morphology and anatomy) is a very important structure in grass classification (Foster, 1966; Thomasson, 1978a, 1978b), especially at the generic level. Foster (1966) used the lemma characteristics to describe the species of Calamagrostis for Bolivia, and Tovar (1960) to describe the species from Peru. They distinguished two groups within the genus Calamagrostis:

1. Lemma distinctly stipitate below the callus, the stipe varying in length (1-4 mm) raising the floret between the glumes (Figs. 1b, 2b, 3b), used here to describe subsection Stylagrostis;
2. Lemma sessile below the callus.

SUBSECTION STYLAGROSTIS

Genus: Calamagrostis; Section: Deyeuxia; subsection: Stylagrostis (Mez) Escalona, stat. nov. Based on Stylagrostis Mez, Bot. Arch. 1:20 (1922). Type: Calamagrostis ovata (Presl) Steud., Nom. Bot. 1:251. (1840). "Hab. in Peruviae montanis huanocensibus." Huanuco, Peru. Haenke (Isotype US 2105044).

Diagnosis: Spikelet: 1-flowered, laterally compressed, floret raised on a lemma stipe, that usually disjoints at the summit, the stipe remaining between the glumes. Endosperm: liquid, soft or hard. Stomata: lacking on the abaxial surface.

Perennials. Culms: erect caespitose or decumbent, 5 cm-1 m tall. Sheaths: long or short, glabrous scabrous. Ligules: 0.5-1.8 mm long, truncate, hyaline or linear, bifid at the apex or linear acuminate. Blades: 2-60 cm long, flat, conduplicate or involute, partially or permanently convolute. Panicle: 2-40 cm long, terminal, lax or spiciform, cylindrical, oval or oblong. Spikelets: 1-flowered, laterally compressed, floret raised on a stipe, this usually disjoints at the summit, the stipe remaining between the glumes. Glumes: 2, persistent, lanceolate acute, coriaceous, membranaceous or hyaline, longer than the floret, equal or the lower shorter, carinate or not, lower 1-nerved, upper 3-nerved. Lemma: rigid, shorter than the glumes, lanceolate, ovate, or truncate, with or without keel, scabrous or glabrous, 5-nerved, 2-4 mm dentate. Awn: subterminal, medial or basal, straight or bent usually twisted or rarely lacking. Callus: pilose (or exceptionally glabrous). Lemma stipe: 1-4 mm long, raising the floret between the glumes. Palea: 2-nerved, 2-keeled, scabrous or glabrous, shorter than the lemma. Ovary: 0.5 mm to 2 mm long, ovate to oblong stigmas plumose, ovate to oblong. Lodicules: two, bilobate, hyaline, glabrous, 0.5-1 mm long. Stamens: 3, anthers linear, from 0.5 mm to 4 mm long, filaments short or long. Caryopsis: ovoid or oblong, persistent, included in the glumes, with liquid, soft, or hard endosperm. Rachilla extension: usually pilose, sometimes glabrous and sometimes reduced, rarely subtending a rudimentary lemma or complete floret. Habitat and distribution: cool regions of the Andes in South America (páramo and puna, 2,500-5,500 m) and probably in temperate and montane environments of

the world.

Subsetion *Stylagrostis* is named after "*Stylagrostis*" novum Graminearum genus published by Carl Mez in *Botanisches Archiv*, 1: 20 (1922). Mez listed 14 species that were primarily described under the genera *Deyeuxia*, *Agrostis*, and *Calamagrostis*, grouping them on the basis of the rachilla extension raising the floret. He transferred these species to the new genus *Stylagrostis*, but did not list a type species nor provide species descriptions. The type species here selected for this subsection is *Calamagrostis ovata* described by Presl in 1830.

SPECIES DESCRIPTIONS

The terminology used to describe microcharacters is adapted from Ellis (1976, 1979).

Calamagrostis cleefii Escalona, sp. nov. Type: COLOMBIA: Meta, Páramo de Sumapaz, en el lado oeste del superpáramo, 4,100 m, 13 Nov., 1973, Antoine Cleef, 7768 (Holotype, US 2785746). Fig. 1.

Perennis. Culmi: erecti, caespitosi (10-25 cm alti) glabri, innovationibus intravaginalibus. Vaginae: 1-2 cm longae, glabrae. Ligula: breves, 0.5 mm longae, membranaceae. Laminae: convolutae, 2-5 cm longae, apicibus acutis, 1 mm latae, paginis adaxialibus glabris minute. Panicula: Pedunculis 6-11 cm longis, laxa 3-6 cm longa, 0.5-1 cm lata, ramis verticillatis. Spiculae: 4 mm longae, lateraliter complanatae, flosculis 3 mm longis, pedicellis glabris. Glumae: 2; subaequales, flavo-purpurascens, glabrae. Gluma I: triplinervis, 4 mm longa. Gluma II: quintuplinervata, 4.5 mm longa. Lemma: 2.2-2.6 mm longa, scabra, quater dentata, hyalina. Arista: 5 mm longa, basalis, scabridus excerta, supra basin contorta. Callus: brevis cuneatus, dense pillosus, 2.3-3.5 mm longus, aliquot lemma superantibus. Stipe lemmatis: 0.2 mm longus. Palea: 2 mm longa, hyalina, binervis, bicarinata, carina scabra. Ovarium: ovatum, flavum, 1 mm longum. Lodiculae: 2; hyalinae. Stamina: 3; antherae 3; 1.5 mm longae, ovatae, flavae. Caryopsis: oblonga teres, brunnea, 1.25 mm longa, scutello per tertiam partem caryopsis aequante, endospermio molli. Extensiones rachillae: 2 mm longae, villosae ab imo ad summum.

Perennial. Culms: caespitose, glabrous, 10-25 cm tall, erect with intravaginal innovations. Sheaths: 1-2 cm long, minutely glabrous. Ligules: short (0.50 mm) and membranaceous. Blades: convolute 2-5 cm long, 1 mm wide, tapering to a point; adaxial surface glabrous. Panicle: peduncle 6-11 cm long, lax, 3-6 cm long, 0.5-1 cm wide, with verticillate branching. Spikelets: laterally compressed, 4 mm long pedicel glabrous, floret 3 mm long. Glumes: 2, sub-equal, yellow-purpuraceous, glabrous. Glume I: 3-nerved, 4 mm long. Glume II: 5-nerved, 4.5 mm long. Lemma: scabrous, four-toothed, hyaline, 2.2-2.6 mm long. Awn: 5 mm long basal, exerted, scabrous, twisted at the base. Callus: short cuneate densely hairy, hairs unequal, distributed all around the callus, 2.3-3.5 mm long, the longest ones exceeding the lemma. Lemma stipe: 0.2 mm long, raising the floret. Palea: 2 mm long, hyaline, 2-nerved, bikeeled (keels scabrous). Ovary: ovate,

yellow 1 mm long. Lodicules: 2, hyaline. Stamens: 3; anthers yellow, 1.5 mm long. Caryopsis: oblongo-terete, brown, 1.25 mm long; scutellum 1/3 as long as the caryopsis; endosperm soft. Rachilla extension: 2 mm long, hairy from base to apex, hairs shorter at the apex.

Microcharacters

Leaf blade: U-shaped in x-section. Adaxial ribs and furrows: six flat, scabrous-topped ribs and five deep narrow furrows, with the sides almost vertical. Stomata: sunken on the adaxial furrows. Medial vascular bundle: the leaf infold divides the blade into two asymmetrical halves. Vascular bundle arrangement: two first order vascular and four second order, located close to the abaxial epidermis, the first order are circular, with the phloem surrounded by thick-walled fibers, protoxylem and metaxylem vessels present. Vascular bundle sheaths: the inner sheath complete, surrounding all vascular bundles, with thicker cells on the abaxial surface; the outer sheath surrounding the inner one, with thin-walled cells. Sclerenchyma: adaxial, absent; in the abaxial surface the epidermal cells become thick, below each first order vascular bundle (1-2 cells thick; 3-5 cells long), sclerenchyma between vascular bundles, absent in the leaf margin, as on the abaxial surface. Mesophyll: irregular cells of different size and shape, tightly packed. Epidermal cells: abaxial outer tangential wall of individual cells, thickened and covered by a distinct, continuous thick cuticle; adaxial; very thin-walled cells with prickles, over the ridges or units. Prickles: on the adaxial epidermis, opposite to the vascular bundles. Silica bodies: horizontally elongate. Blooming: Nov.-Feb. Habitat and distribution: wet places of the superpáramo in Colombia. The major limitation in considering this species is the lack of sufficient specimens. Only one specimen was observed, the type. However, the type showed characters that differ from the other Calamagrostis species inhabiting the same or surrounding areas. This species resembles Calamagrostis pisinna but differs in the number of vascular bundles in the leaf blade cross section (6) and reduced sclerenchyma. Calamagrostis cleefii: is characterized by infolded leaves, and a two-keeled scabrous palea. The leaf cross-section shows six furrows and seven ridges, vascular bundles with two well-distinguished bundle sheaths, the inner with half of each cell thickened. This species grows in tufts in boggy places of the superpáramo, 4,100 m in Colombia.

Calamagrostis guamanensis Escalona, sp. nov. Type: ECUADOR: Prov. Napo, Road Quito-Baeza at the telecommunication antenna, north of the Guamani páramo, in the oriental Andes. Grass forming loose tufts in cushion plants of Distichia muscoides, 4,260 m (78° 09' W, 0° 17' S), March 3, 1985, F. Escalona and S. Gallegos 390 (Holotype ISC, Isotypes MO, K, QCA, US, VEN). Fig. 2.

Perennis. Culmi: teretes, erecti, (6-15 cm alti) innovationibus intravaginalibus, 6-15 cm alti. Vaginae: apertae, 2-5 cm longae, fibrosae, glabrae, albae, glaucae. Ligulae: brevis, truncata, glabra 1 mm longa, membranacea. Laminae:

plicata, inflata basin versus, 2-8 cm longa, 2-3 cm lata, paginis abaxalibus glabri, scabra, marginibus sacbris. Panicula: panicula aperta laxa, 5-8 cm longa, 1-2 cm lata, rachis glabra, pedunculus foliis excedens 7-11 cm longus. Spicula: complanata lateraliter 4 mm longa, pedicellis glabris. Glumae: 2; 4-5 mm longae, triplinervis, purpuratae ad apicem. Lemma: 2.5-3 mm longum, quadridentatum, fissura ad dimidium carinae attingens. Arista: recta vel flexuosa, incisura lemmatis exoriens scaberula, 7-8 mm longa. Callus: brevis pilosus aequaliter ad dimidium lemmatis attingens. Stipes lemmatis: capitatus, 1 mm longus. Palea: hyalina, 2 mm longa, carina scabrosa. Ovarium: ovatum, flavum, 1 mm longum. Lodiculae: 2, hyalina. Stamina: 3; antherae 3, purpuratae flavascentes, 1 mm longae. Caryopsis: ovata, embryo recto, endospermio liquido. Extensio rachillae: 2 mm longa, capitata e basi pilose dense, pilis 2 mm longis.

Perennial. Culms: growing in loose tufts among the cushion plants, 6-15 cm tall, erect with intravaginal innovations. Sheaths: open, fibrous, 2-5 mm long, glossy-white. Ligules: short, truncate, glabrous, membranaceous, 1 mm long. Blades: folded, medial vascular bundle distinguishable, 2-8 cm long, 2-3 mm wide; blade-sheath junction swollen, abaxial surface glabrous, with margin scabrous. Panicle: an open loose panicle, 5-8 cm long, 1-2 cm wide, rachis glabrous, peduncle exceeding the leaves, 7-14 cm long. Spikelets: laterally compressed, 4 mm long, pedicels glabrous. Glumes: 2; 4-5 mm long, 3-nerved, purple at the apex; Lemma: 2.5-3 mm long, (split half way at the keel), scabrous, 4-toothed. Awn: straight or curved, arising from the lemma notch, scabrous, 7-9 mm long. Callus: short, cuneate, evenly hairy, half as long as the lemma. Lemma stipe: capitate, 1 mm long. Palea: hyaline, 2 mm long, scabrous on the keels. Ovary: ovate and yellow, 1 mm long. Lodicules: 2, hyaline. Stamens: 3; anthers 1 mm long, purple. Caryopsis: ovate, embryo straight, endosperm liquid. Rachilla extension: capitate, 1.5 mm long, densely hairy from the base, terminal hairs exceeding the floret (2 mm long), reducing their size through the rachilla apex.

Microcharacters

Leaf blades: outline V-shaped, not permanently infolded. Adaxial ribs and furrows: ribs 11, square, flat-topped, sides angled, over all vascular bundles, furrows 10, narrow, with sides almost vertical and base fairly broad. Stomata: sunken in the furrows. Medial vascular bundle: distinguishable from the rest by size and position, sclerenchyma girder interrupting the outer vascular bundle sheath on the adaxial surface and strand of sclerenchyma on the abaxial surface, protoxylem and metaxylem present. Vascular bundle arrangement: 5 first order, 3 second order and 2 third order, the ribs over first and second order vascular bundles have flat tops, and those over 3rd order are triangular. All vascular bundles are located closer to the abaxial surface. Vascular bundle sheath: first and second order vascular bundles have inner sheath complete with cell walls thicker on the abaxial surface, outer sheath complete, third order vascular bundle with complete inner sheath but incomplete outer sheath.

Sclerenchyma: adaxial, represented by very small girders, usually not altering the epidermal cells; abaxial, represented by well-developed strands, wider than deep straight, horizontal; sclerenchyma between vascular bundles absent; in the leaf margin as a pointed cap (2-3 cells thick). Mesophyll: chlorenchyma with horizontal arrangement in the mesophyll, U-shaped between successive vascular bundles located at the base and sides of the furrows. Epidermal cells: abaxial epidermal cells with outer tangential wall thickened individually, smooth surface. Prickles: located between typical epidermal cells on the sides of the furrows. Silica cells: elongated, up to 1 mm long with sinuous edges and concave surface, located over the ribs on the adaxial surface. Blooming: October-March. Habitat and distribution: forming loose tufts in the cushions of Distichia muscoides and Plantago sp., endemic to the Guamani páramo in Ecuador, (4,100-4,200 m). Other specimens examined: ECUADOR: Prov. Napo, Road Quito-Baeza (páramo de Guamani, 4,260 m, 78° 09' W 0° 17' S). Oct. 11, 1976, B. Ollgaard & H. Balslev 10111 (MO, FM). Road Quito-Baeza, (páramo de Guamani), 4,260 m, 78° 09' W 0° 17' S), Nov, 1978, 4,000 m, Simon Laegaard 53,861 (AAU). Prov: Ibarra. Dept. Imbabura, May 9, 1954; 4,600 m. Rauh and Hirsh E153 (US).

Calamagrostis quamanensis forms loose tufts in cushions of Distichia muscoides and Plantago. It is endemic to Guamani páramo in Ecuador. C. quamanensis is characterized by a swollen sheath-blade junction, well-distinct leaf venation pattern, fibrous sheath, leaf cross-section outline V-shaped, 11 vascular bundles, and a drooping panicle. All the analyses (numerical and cladistic) revealed this species as new, no species presenting these features having been described for Ecuador. It resembles Calamagrostis ramonae, another new species found in Venezuela.

Calamagrostis ramonae Escalona, sp. nov. Type: VENEZUELA. Merida, near upper limit of paramo around the small lake between Chachopo and Los Apartaderos near El Aguila, April 15, 1944, 3,930 m, J. Steyermark 55903 (Holotype, F 1206466; Isotype US 1869496). (Fig. 3).

Perennis. Culmi: erecti, caespitosi, innovationibus intravaginalibus, 30-50 cm alti. Vaginae: 8-11 cm longae, fibrosae, albae, scabrae. Ligula: 0.5 mm longa, truncata, hyalina. Laminae: planae, inflatae basin versus, 8-19 cm longae, 3-4 mm latae, paginis adaxialis scabris minute, paginis abaxialis glabris. Panicula: 45-65 cm longa, 1.5 cm lata, laxa, cernua. Spiculae: 4-5 mm longae, pedicellis scabridisculis. Glumae: 2; 3-4 mm longae, triplinervis, pallide virides, acutae vel subacuminate, carinis scabris. Lemna: 3.5 mm longum, angustum, quinquenerve, scabrum. Arista: 5 mm longa, ad medium inserta, infrageniculata, contorta, flexa introrsum. Callus: elongatus, pilis verticillatis, 0.5 mm longus. Stipes lemmatis: 0.5 longus, noncapitatis. Palea: 3 mm longa, scabra, hyalina, binervis, bicarinata. Ovarium: ovatum flavobrunneum, 1 mm longum. Lodiculae: 2, hyalinae. Stamina: 3; antheris luteis, 0.5 mm longis. Caryopsis: oblonga teres, 1 mm longa, endospermio molli.

Extensio rachillae: 3 mm longa, pilis 1-2 mm longis, verticillatis.

Perennial. Culms: 30-50 cm tall, erect, caespitose, innovation intravaginal. Sheaths: 8-11 cm long, fibrose, scabrous, white. Ligules: 0.5 mm long, truncate, hyaline. Blades: flat, 8-19 cm, 3-4 mm wide, blade-sheath junction swollen, glabrous abaxially, minutely scabrous adaxially. Panicle: lax, drooping, 45-65 cm long, 1.5 wide. Spikelets: 4-5 mm long, peduncle scabridulous. Glumes: 3-4 mm long, 3-nerved, light green, keel scabrous, acute to subacute. Lemma: 3.5 mm long, 5-nerved tapering, scabrous. Awn: insertion medial twisted and bent inward, 5 mm long, geniculata below. Callus: elongated, with whorled hairs, 0.5-1 mm long. Lemma stipe: 0.5 mm long. Palea: 3 mm long, scabrous, hyaline, two-nerved, two-keeled (scabrous). Ovary: ovate yellow-brown, 1 mm long. Lodicules: 2, hyaline. Stamens: 3; anthers 0.5 mm long. Caryopsis: elongate, 1 mm long, endosperm soft. Rachilla extension: 3 mm long with 1-2 mm, whorled hairs.

Microcharacters

Leaf blade: V-shaped, with open angle over 90° arms straight, symmetrical on either side of the median vascular bundle. Adaxial ribs and furrows: ribs, 11 flat-topped, square, associated with the vascular bundles; furrows 10 with almost vertical sides, bases fairly broad, located between all vascular bundles. Stomata: sunken on the adaxial furrows. Medial vascular bundle: distinguishable from the other 1st order vascular bundles by medial position. Vascular bundle arrangement: 5, 1st order, associated with sclerenchyma girders adaxially and abaxially, 4 second order, associated with sclerenchyma strands adaxially and abaxially, 2 third order on the leaf margins, associated with sclerenchyma strands; 1st and 2nd order alternate, at the same level in the center of the blade. Vascular bundle sheath: inner sheath cell wall evenly thickened, the outer sheath hardly noticeable. Sclerenchyma: adaxial, inversely anchor-shaped (3-5 cells thick); abaxial, very small girders with epidermal cells not altered under girders; very small (1-2 cells thick) strands below the marginal vascular bundles; between vascular bundles, absent, leaf margin, absent. Mesophyll: irregular; cells of different size and shape; often with intercellular air spaces. Epidermal cells: adaxial, thin-walled cells associated with bundles and papillae; abaxial, very irregular shaped cells thin-walled cells, smooth surface. Prickles: pointed, located between epidermal cells, over the ribs. Silica bodies: horizontally elongate. Blooming: April-December. Habitat and distribution: bogs and humid places in the paramos of Only two specimens of this species were studied, the holotype and the isotype, collected by Steyermark in the Andes of Venezuela. It is obvious that and more field work is needed. C. ramonae is segregated as a different species from the rest of the group, both in cladistic and cluster analysis. It is characterized by well-developed rachilla extension, equaling the palea, with twisted hairs, and elongate callus with twisted hairs. In common with C. guamanensis from Ecuador, this species exhibits a swollen blade-

sheath junction.

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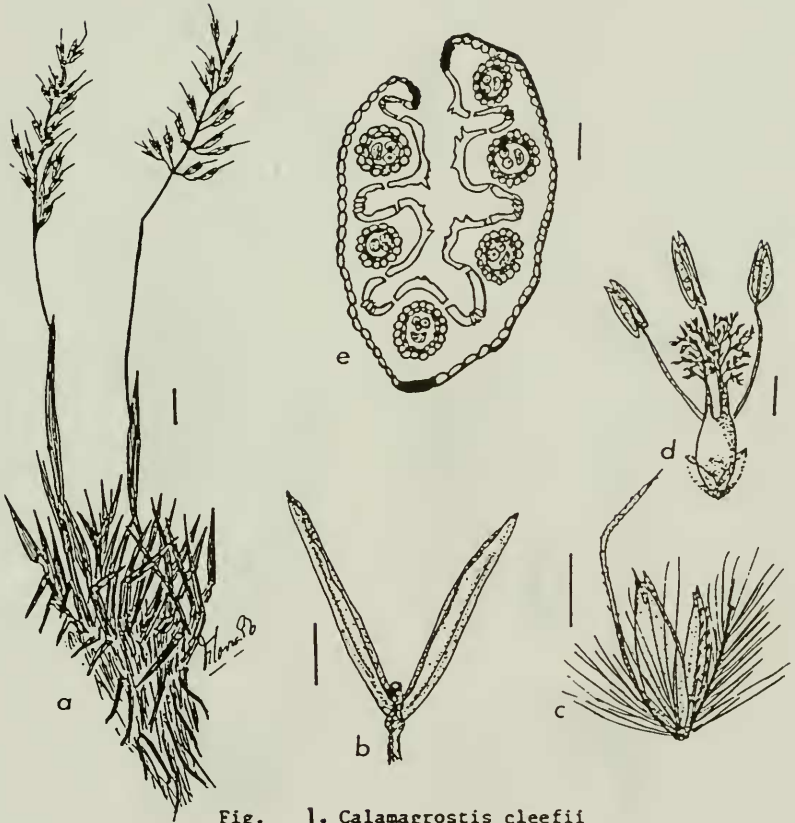


Fig. 1. Calamagrostis cleefii

a. Plant. Bar = 1. cm

b. Glumes and lemma stipe. Bar = 1.62 mm

c. Floret. Bar = 2 mm

d. Ovary and anthers. Bars = 1 mm

e. Leaf blade cross section. Bar = 1 mm

Based on Cleef 7768

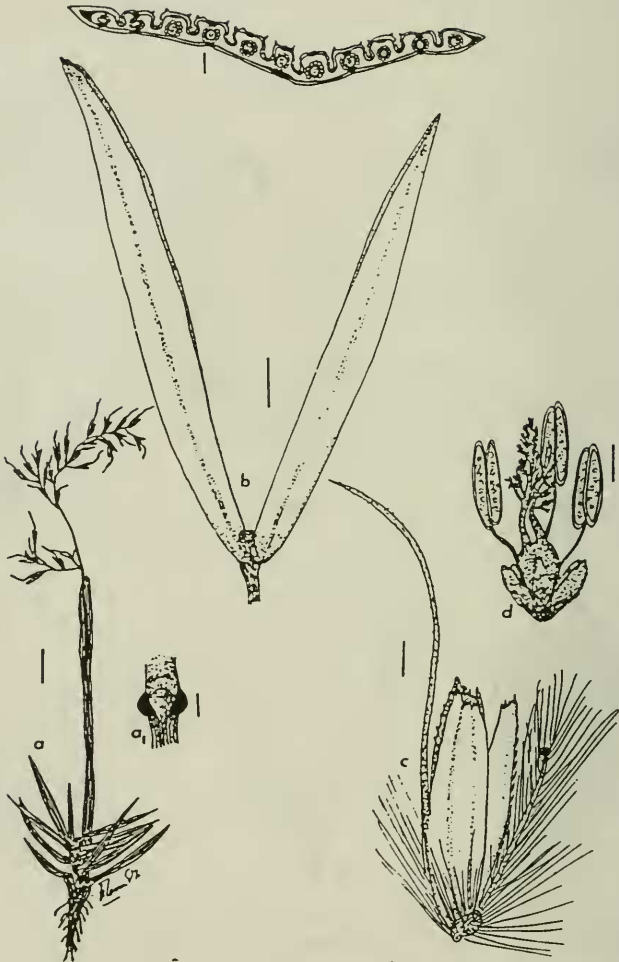


Fig. 2. *Calamagrostis guamanensis*

- a. Plant. Bar = 1.4 cm. Laegaard 54508
- a1. Swollen junction between leaf blade and sheath. Bar = 1 cm Escalona et al. E390.
- b. Glumes and lemma stipe. Bar = 4 mm. Ollgaard et al. 10111
- c. Floret. Bar = 3 mm. Ollgaard 10111
- d. Ovary and anthers. Bars = 3 mm. Ollgaard et al 10111
- e. Leaf blade cross-section. Bar = 5.6 mm. Escalona et al. E390

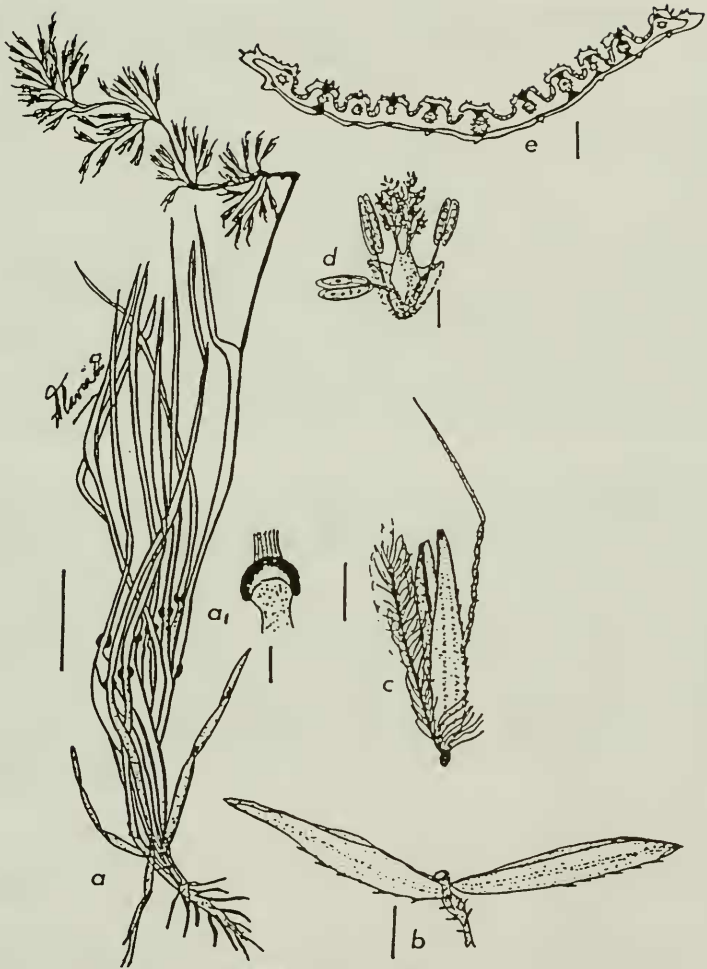


Fig. 3. *Calamagrostis ramonae*

- a. Plant. Bar = 6.6 cm
 a1. Swollen junction between the sheath and the blade
 b. Glumes and lemma stipe. Bar = 1.5 mm
 c. Floret. Bar = 1.7 mm
 d. Ovary and stamens. Bar = 2 mm
 e. Leaf blade cross-section. Bar = 4.3 mm

Based on Steiermark 55903